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Competition thresholds for the survival and growth of ponderosa pine seedlings associated with woody and herbaceous vegetation

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Application. A quantitative understanding of the competitive influence of woody and herbaceous vegetation on young conifers is required to make appropriate vegetation management decisions in new plantations. Knowing the biological thresholds of competition for the survival and stem-volume growth of conifer seedlings, such as ponderosa pine, can provide a basis for evaluating the need and objectives for vegetation control treatments.

Abstract. Patterns of survival and stem-volume growth for planted seedlings of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) competing with various levels of woody and herbaceous vegetation were derived from three previous studies—one in Oregon and two in Montana. Negative hyperbolic curves of opposite concavity describe the relation between the abundance of woody or herbaceous vegetation and (1) the survival and (2) the stem volume of the pine seedlings. From these curves, two types of competition thresholds for managing forest vegetation are identified: (1) maximum-response threshold—a level of vegetation abundance where additional control measures will not yield an appreciable increase in tree performance; and (2) minimum-response threshold—a level of vegetation abundance that must be reached before additional control measures will yield an appreciable increase in tree performance. The maximum- and minimum-response thresholds for pine stem volume occurred at lower levels of vegetation abundance than those for pine survival. Thus, forest managers may need to consider ponderosa pine survival and stem-volume growth as separate objectives when managing woody and herbaceous vegetation in young plantations. Knowledge of maximum- and minimum-response thresholds also can be used to improve herbicide prescriptions.

Introduction

Woody and herbaceous plants can seriously threaten the survival and growth of conifer seedlings through interspecific competition for light, water, and nutrients (Walstad and Kuch 1987). Therefore, vegetation management is an important silvicultural consideration. Stewart et al. (1984) have described over 200 studies that show vegetation manipulation improves tree growth and/or survival. These studies reported stand-volume growth increases of 40 to 100% when competing vegetation was controlled (Stewart 1987). The increases in tree growth were related to the degree of vegetation control despite a wide range of conifer species, vegetation types, stand conditions, environments, and control methods.

Models that can predict tree survival and growth under various levels of interspecific competition, however, are not widely available (Tappeiner and Wagner 1987; Walstad and Kuch 1987), perhaps because most research on forest vegetation management has focused on comparing different control methods. Although such studies can help researchers develop new technology and demonstrate how vegetation management improves stand survival and growth, they have not provided a quantitative basis on which foresters can evaluate the need or objectives for vegetation management treatments. Consequently, most treatment decisions are based on subjective standards (Tappeiner and Wagner 1987; Walstad and Kuch 1987). Models of interspecific competition analogous to those developed for managing stand density or intraspecific competition (Reineke 1933; Drew and Flewelling 1977, 1979; McCarter and Long 1986) are needed.

Entomologists first used threshold concepts to improve pest management decisions (Stern et al. 1959). The "economic-injury level" (the pest density at which the value of the crop loss equals the cost of treatment) and the "economic threshold" (the pest density at which control measures should be taken to prevent an increasing pest population from reaching the economic-injury level) are now fundamental principles of integrated pest management (Norgaard 1976; Thomas et al. 1979; Matthews 1984). Threshold concepts in weed management also need to be developed for both agricultural and forest crops (Radosevich and Holt 1984; Walstad and Kuch 1987). Establishing these thresholds, however, is a difficult task that requires the ability to make several complex biological and economic predictions (Cussans et al. 1986). The most difficult prediction is assessing the effect that the weed population will have on the crop (Walstad and Kuch 1987).

In the research reported here, we used results from three previous studies—one in Oregon and two in Montana—to quantify the relation between various levels of woody and herbaceous vegetation, and the survival and growth of planted seedlings of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). These relationships were examined to determine whether competition thresholds were apparent, and whether pine survival and growth responded differently to interspecific competition. A "competition threshold" is defined here as a level of vegetation abundance where there is an abrupt increase or decrease in the rate of change of a response variable.

Methods

At an Oregon location (Study 1), the effects of various levels of woody vegetation on the survival and stem-volume growth of pine seedlings were evaluated 8 years after six site-preparation treatments were applied (Ross et al. 1986). The study was designed to compare the responses of seedlings planted in 1976 to these treatments, which resulted in various degrees of physical site disturbance and shrub recovery.

At a site near Missoula, Montana (Study 2), first-year survival of pine seedlings associated with various levels of herbaceous vegetation was studied (Petersen and Maxwell 1988). A gradient of herbaceous leaf area along rows of planted pine seedlings was created with a herbicide application in 1984.

At a site near Kalispell, Montana (Study 3), various levels of herbaceous vegetation surrounding individual pine seedlings were studied for herbicide-treated and untreated areas (Petersen 1987). Three growing seasons after the seedlings were planted in 1981, the stem-volume growth and projected leaf-area index of surrounding herbaceous vegetation were calculated for each surviving tree.

Study 1

The East Aspen site is 14 km from Klamath Falls, Oregon, on the Klamath Tree Farm of the Weyerhaeuser Company. It is on the east side of the Cascade Range at an elevation of 1370 m. The soil is a moderately deep, stony, clay loam derived from volcanic ash over basalt (Duncan and Steinbrenner 1975). Summers are hot and dry, and nearly all of the annual precipitation occurs during the winter (Franklin and Dyrness 1973).

Six site-preparation treatments (logging only, ripping, disking, brush-blading, herbicide spraying, and herbicide spraying followed by disking) were applied in 1975 and 1976 to control woody and herbaceous vegetation growing on the site. The predominant shrub species included snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), bitter-brush (*Purshia tridentata* (Pursh) DC.), cherry (*Prunus* spp.), serviceberry (*Amelanchier* spp.), snowberry (*Symphoricarpos* spp.), and rose (*Rosa* spp.).

Recovery of herbaceous vegetation involved mainly grasses, and averaged about 35% cover over all the treated areas. Because the recovery did not differ significantly between the treatments (Ross et al. 1986), herbaceous vegetation levels were considered a constant background influence in this study.

A randomized, complete block split-plot design was used for the study. Each main plot, which measured 24.4 × 54.9 m, was treated by one of the procedures described above. The treatments were replicated on two blocks within the study site. In spring, 1976, 100 ponderosa pine seedlings (2+0 bareroot or 1+0 plug) were planted 1.2 m apart in a grid pattern in each of two subplots per plot. These subplots measured 24.4 × 6.1 m. Seedlings planted in the area treated by ripping were placed in rows parallel to the long axis of the main plot.

In 1983 (8 years after the site-preparation treatments), shrub regrowth as well as pine survival and size were measured. In all but the ripped plots, transects 2 × 15 m were established diagonally across each subplot. In the ripped plots, transects 2 × 60 m were established diagonally across each main plot. Equal ground area was sampled on all plots. The height and crown width of each shrub within a transect were measured and then used in regression equations to predict its biomass (Ross and Walstad 1986a). Only the inner 40 tree seedlings on each subplot were sampled; the remaining ones were left as a buffer. Tree survival for each subplot was calculated as the percentage of the original seedlings still alive. Total height and stem diameter were measured for each surviving tree. Because no difference was found between the survival and growth of the bareroot seedlings and that of the plugs (Ross et al. 1986), the results were combined from both types for this study. A stem volume index (V) was calculated for each tree in the subplot with the equation $V = D^2H$, where D = stem diameter (outside bark) at 10% of total height, and H = tree height.

Study 2

Located about 40 km from Missoula, Montana, this site is at 1,480 m elevation and has a southern aspect with 5% slope. The soil is a silt loam 10 to 30 cm deep. Summers are hot and dry, with most of the annual precipitation occurring during the winter. Before the pine seedlings were planted, a dense stand of pinegrass (*Calamagrostis rubescens* Buckl.), elk sedge (*Carex geyeri* Boott), thistle (*Cirsium* spp.), knapweed (*Centaurea maculosa* Lam.), creeping western barberry (*Berberis repens* Lindl.), kinnikinnick (*Arctostaphylos uva-ursi* [L.] Spreng.), and snowberry (*Symphoricarpos albus* [L.] Blake) dominated the site.

On May 12, 1984, a continuous gradient of herbaceous leaf area was created by application of the herbicide hexazinone (3-cyclohexyl-6-(diethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)dione) with a logarithmic sprayer (Yates and Ashton 1960) to plots 5.5 × 13 m. The sprayer applied a constant volume of spray mix (467 L/ha), but logarithmically decreased the concentration of hexazinone as distance traveled along the plot increased. The sprayer was calibrated to deliver a continuous gradient of hexazinone that ranged from 0.3 to 3.4 kg a.i./ha on each plot. Three replications of the hexazinone gradient were established on the site. The direction of the gradient was randomly determined on each plot.

On May 14—15, 1984, 84 bareroot, 2+0 ponderosa pine seedlings from a local seed source were planted in 12 rows along each hexazinone gradient. Each row contained seven seedlings spaced 0.3 m apart and was oriented perpendicular to the direction of the gradient. The rows were spaced 1 m apart along the gradient. The last two rows in each plot were outside the treated area. The treated area extended 1.25 m beyond the first and last seedling in each row.

In July, 1984, when the herbaceous leaf area had reached maximum development, the projected leaf-area index was measured at each seedling row with a point-intercept frame (Mueller-Dombois and Ellenberg 1974). This 1-m-long frame with 10 pins spaced 0.1 m apart was systematically placed at 9 positions on the ground around each row of seedlings. Each pin on the frame was moved vertically down through the canopy, and the number of intercepts that each pin made with live foliage was recorded. This technique measured the projected leaf-area index, an underestimate of actual leaf-area index, because leaf angle was not considered.

Seedling survival was recorded at the end of the first growing season in September, 1984. Survival along each hexazinone gradient was calculated as the percentage of the original 14 seedlings in two adjacent rows that were still alive. Mean projected herbaceous leaf-area index was calculated for the two rows of seedlings.

Study 3

The site is 35 km west of Kalispell, Montana, at an elevation of 1,330 m. It has a south aspect with a 20 to 30% slope. The soils are a silt loam 10 to 30 cm deep. As in studies 1 and 2, the summers are hot and dry with most of the annual precipitation occurring during the winter.

Thirty bareroot, 2+0 ponderosa pine seedlings were planted on each of six plots in March, 1981. Each plot consisted of 2 rows, each with 15 seedlings equally spaced 2 m apart. A randomized, complete block design was used for the study, with three replications. Three plots were treated with hexazinone (2.0 kg a.i./ha in a 467 L/ha aqueous spray) 2 weeks after the seedlings were planted. A 2-m buffer was sprayed around each plot. Three plots were left unsprayed. The site was dominated by pinegrass, elk sedge, arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.), and thistle. Thus, a range of herbaceous vegetation abundance around individual trees resulted on herbicide-treated and untreated plots.

In September, 1983, after three growing seasons, the total height and stem diameter at the base of all surviving trees was measured. A stem volume index was calculated using $V = D^2H$. The projected herbaceous leaf-area index also was measured on two sides of each tree with a point-intercept frame as in Study 2. The frame was placed on an east-west orientation 0.5 m from the north and south sides of the tree stem. Projected herbaceous leaf-area index was averaged for each tree from the two sampling points.

Analytical approach

For each study, percent survival and stem volume were transformed to the percentage of a maximum observed value to hold the units of the response variables constant. Percent of maximum survival and stem volume for Study 1 was expressed relative to the maximum subplot value observed within each of the two replications. Percent of maximum survival in Study 2 was expressed relative to the maximum survival observed in the two-row subplot of each replication of the hexazinone gradient. Percent of maximum stem volume in Study 3 was expressed relative to the largest individual tree observed in the study.

Linear regression analysis was used to examine the quantitative relation between the percent of maximum survival or stem volume, and the shrub biomass or projected herbaceous leaf-area index. Transformation of variables was used where appropriate to correct for nonlinearity and nonconstant variances. The final regression models were selected based on the adjusted r^2 and analysis of the residuals.

Results

Tree survival

Tree survival decreased as shrub biomass increased in Study 1 (Fig. 1A). Survival also decreased as the projected leaf area of herbs in Study 2 became greater (Fig. 1B). Negative hyperbolic curves with downward concavity describe the relationships in both studies. Interspecific competi-

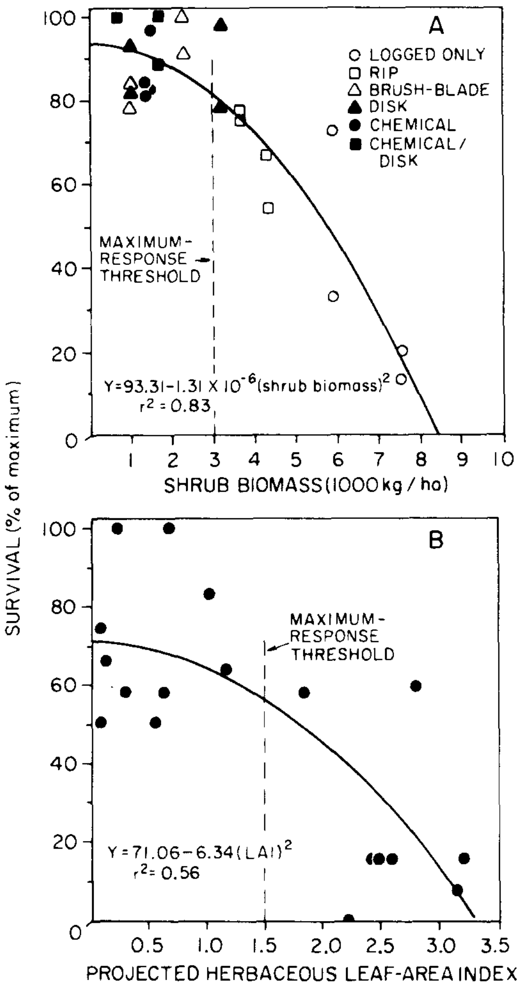

Fig. 1. Percent of maximum survival for (A) 8-year-old ponderosa pine seedlings growing with various levels of shrub biomass in south-central Oregon after six site-preparation treatments (Study 1), and (B) 1-year-old pine seedlings growing with various levels of herbaceous vegetation in western Montana (Study 2). Vegetation levels below the "maximum-response threshold" were not associated with appreciable increases in pine survival.

tion accounted for 83% of the variation in tree survival in Study 1 and 56% of the variation in Study 2. The lower correlation between tree survival and vegetation abundance in Study 2, relative to Study 1, may have been related to fewer trees per plot (14) and only one growing season available for survival patterns to emerge.

The shape of the curves suggests that most losses in pine survival were associated with vegetation levels above 3,000 kg/ha shrub biomass in

Study 1 and 1.5 projected herbaceous leaf-area index in Study 2. Actual maximum survival was greater than 90% in Study 1 and 85% in Study 2. The relatively flat shape of the curves, below 3,000 kg/ha shrub biomass and 1.5 projected herbaceous leaf-area index, suggests that appreciable increases in pine survival were not achieved by controlling competing vegetation below these levels. Thus, a competition threshold for achieving maximum survival (a "maximum-response threshold") was subjectively determined to occur at these levels of vegetation abundance (Fig. 1).

Stem volume

The percent of maximum stem volume was correlated negatively for 8-year-old pine seedlings with shrub biomass (Study 1) (Fig. 2A) and for 3-year-old pine seedlings with projected herbaceous leaf-area index (Study 2) (Fig. 2B). The relation between the percent of maximum stem volume and shrub biomass can be described by a negative hyperbolic curve with upward concavity (Fig. 2A). Shrub biomass accounted for 77% of the variation in stem volume. Conventional regression analysis of individual-tree stem volume and surrounding herbaceous leaf area provided an unsatisfactory description of data from Study 3. A negative hyperbolic curve with upward concavity also describes the upper boundary of the scatter plot of stem volume and leaf area (Fig. 2B). Many small trees that had low leaf-area values limited the accurate description of tree size with regression analysis. Alternately, a boundary line (Webb 1972; Chambers et al. 1985) was drawn describing the upper limit of the relationship between percent of maximum stem volume and projected herbaceous leaf-area index.

The shape of the curves indicates that maximum stem volume occurred where shrub biomass and herbaceous leaf area were near zero. It was not possible to identify maximum-response thresholds for pine stem volume from these data; however, this threshold is likely to be very near zero levels of vegetation abundance.

Most losses in pine stem volume occurred at vegetation levels under 3,000 kg/ha shrub biomass and 0.5 projected herbaceous leaf-area index. Little change in stem volume occurred when competing vegetation was managed above these levels. Thus, a second type of competition threshold for achieving any appreciable response in pine stem volume (a "minimum-response threshold") was subjectively assessed to occur near 3,000 kg/ha shrub biomass and 0.5 projected herbaceous leaf-area index (Fig. 2). Substantial gains in pine stem volume from vegetation management would require treatments that reduced vegetation abundance below the minimum-response threshold.

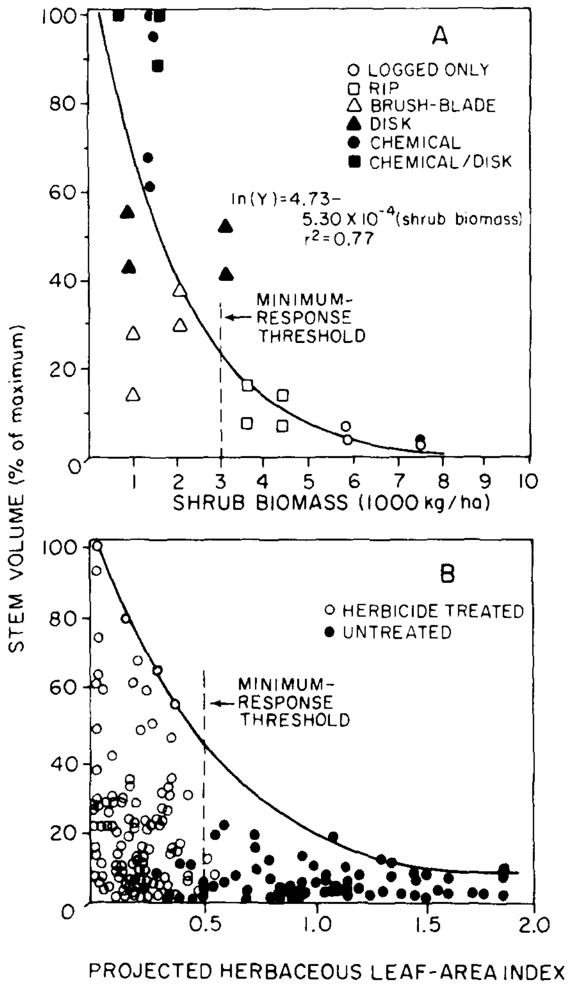

Fig. 2. Percent of maximum stem volume for (A) 8-year-old ponderosa pine seedlings growing with various levels of shrub biomass in south-central Oregon after six site-preparation treatments (Study 1), and (B) individual 3-year-old pine seedlings surrounded by various amounts of herbaceous vegetation in western Montana (Study 3). The "minimum-response threshold" identifies the level of competing vegetation that needed to be achieved before vegetation treatments were able to yield an appreciable increase in pine stem volume.

Discussion

Effects of interspecific competition on seedling growth and survival

Reduced growth and survival for young ponderosa pines associated with shrubs (Barrett 1982; Oliver 1984; Lanini and Radosevich 1986;

Shainsky and Radosevich 1986; White 1988) and herbaceous vegetation (Tappeiner and Radosevich 1982; White 1988) have been consistently documented (Ross and Walstad 1986b). Shrub and herb abundance is often associated with increased depletion of soil water and leads to high moisture stress in pines during the growing season (Lanini and Radosevich 1986; Shainsky and Radosevich 1986; White 1988). Petersen and Maxwell (1987) found that the predawn needle water potential of ponderosa pine and the soil water content were negatively correlated with the projected herbaceous leaf-area index along the hexazinone gradients established in Study 2. Competition for available soil nitrogen between tree seedlings and herbaceous vegetation also may influence tree growth and survival (Elliott and White 1987).

Negative hyperbolic curves, similar to those reported here describing the relation between maximum stem volume of ponderosa pine trees and shrub abundance (Study 1) (Fig. 2A), have been reported in other studies (Oliver 1984; Powers and Oliver 1985). Similar relationships also have been derived for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and loblolly pine (*Pinus taeda* L.) growing with various levels of woody vegetation (Walstad 1976; Burkhart and Sprinz 1984; Brand 1986, Wagner and Radosevich 1987). Curves describing agricultural yield losses under increasing weed density also consistently display a similar shape (Cousens 1987). The negative hyperbolic relation between individual tree size and the density of neighboring shrubs and herbs is consistent with the reciprocal-yield law (Shinozaki and Kira 1956), which has been repeatedly demonstrated for a wide range of plant species (Harper 1977). There are exceptions, however; negative linear relationships between conifer growth and competitor density also have been reported (Lewis 1981; Zutter et al. 1986, Chan and Walstad 1987, White 1988).

Interpreting the effects of interspecific competition on pine stem volume was influenced by whether the analysis was based on plot means or individual trees. Although conventional regression analysis provided a satisfactory description of plot means (Fig. 2A), it was unsatisfactory for individual trees (Fig. 2B). Interspecific competition appeared to set an upper limit on the potential growth of individual trees. Lower leaf area of competitors provided the opportunity for greater tree growth, but did not insure that it would occur. At projected herbaceous leaf-area index values above 0.5 (the minimum-response threshold), interspecific competition appeared to be the most important factor limiting tree growth. Potential stem volume was reduced by 75% or more. Below the minimum-response threshold, some trees were able to achieve a higher level of growth, but many appeared to be limited by other factors. Factors other than interspecific competition that might account for the type of variation shown in

Fig. 2B include initial seedling size, genetic variation, soil compaction, herbivory, pathogens, herbicide injury, and seedling vigor at the time of planting. Petersen (1988) describes how the frequency distribution of individual tree size changes with competition from herbaceous vegetation in Study 3. Statistical limitations of regression analysis for describing individual plant size in relation to measures of stand density also have been noted by others (Waller 1981; Liddle et al. 1982; Firbank and Watkinson 1987).

Tree survival remained constant and relatively high at levels of competing vegetation that caused stem volume to decrease rapidly (Figs. 1 and 2). Survival did not decline until stem volume was reduced to less than 25% of the observed maximum. The opposite hyperbolic shape of the survival and stem-volume curves suggests that pine growth decreases first as competitive stress is encountered. Once environmental resources are depleted beyond the ability of the seedling to plastically decrease growth much further (the stem-volume minimum-response threshold), survival is threatened. Increasing competitive stress beyond the minimum-response threshold for growth will increase the probability of mortality in the seedling population (the maximum-response threshold for survival). No minimum-response threshold for pine survival was apparent under the range of competition levels evaluated, although such a threshold should theoretically exist. A hypothetical model of the relationships between the

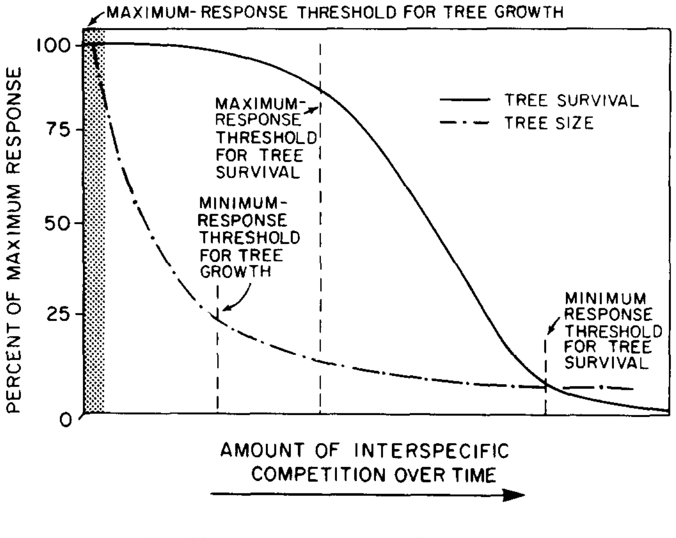

Fig. 3. Hypothetical relationship between interspecific competition, and tree survival and growth. The maximum- and minimum-response thresholds for tree survival and growth occur at different levels of interspecific competition. The maximum-response threshold for tree growth occurs in the shaded region under nearly vegetation-free conditions.

maximum- and minimum-response thresholds for conifer survival and growth is presented in Fig. 3. Although conifer survival patterns under various levels of interspecific competition have not been widely studied, a negative hyperbolic curve with downward concavity also describes loblolly pine survival in relation to hardwood basal area (Burkhart and Sprinz 1984).

Although we correlated tree survival in Study 1 with shrub biomass in 1983—8 years after the site-preparation treatments—most of the pine mortality occurred within the first two growing seasons after planting (Ross 1985). Because no vegetation measurements were taken at this time, it was not possible to evaluate this relationship immediately after planting. We have assumed that a correlation between shrub biomass in 1983 and pine survival exists because vegetation levels in that year are correlated with vegetation levels during the first few years after planting. Although the relative shape of the survival curve (Fig. 1A) may have been the same, the shrub biomass at the maximum-response threshold for survival (3,000 kg/ha) was probably lower in the first 2 years after planting. Undocumented differences in herbaceous vegetation also may have influenced tree survival immediately after planting.

Management implications

On the dry sites we studied, vegetation management treatments under high levels of competition were likely to increase tree survival before they increased growth. The maximum-response threshold for pine survival did not occur until nearly half of the potential shrub or herb density was removed. The minimum-response threshold for stem volume occurred at vegetation levels near or under that of the maximum-response threshold for survival.

Under nearly vegetation-free conditions, where maximum tree growth was observed, all of the environmental resources of a site are available for tree growth (Radosevich and Osteryoung 1987). Even small amounts of woody or herbaceous vegetation can deplete significant amounts of the available resources, thus reducing tree growth. Oliver (1984) also noted that the maximum periodic annual stem-diameter increment for ponderosa pine was not achieved until all neighboring shrubs were removed. Shrub coverage had to be less than 20 to 30% before a minimum-response threshold for diameter increment was achieved.

Although it is technologically feasible to create nearly vegetation-free conditions in young forest plantations by intensive use of site-preparation treatments and repeated herbicide applications, the environmental and economic desirability of such practices for extended periods of time requires careful consideration. Silvicultural prescriptions to achieve vegetation-free conditions also may be inconsistent with some multiple-use forest management objectives. For example, forage for domestic animals or wildlife also is a desired forest product in many ponderosa pine plantations.

Because the cost of achieving lower levels of competing vegetation to increase pine growth rates may generally be higher than the cost of managing vegetation for maximum survival, pine growth and survival may need to be considered as separate forest management objectives. Managing for a maximum-response threshold of conifer survival may be easier to justify economically than managing for increased growth because

— reduced survival can delay regeneration (Brodie and Tedder 1982; Straka and Hotvedt 1985) and
— replanting requires an additional investment.

Separating growth and survival as management objectives also may be important if forest managers divide lands into areas that are to be intensively and extensively managed (Atkinson 1986).

One of the major obstacles to prescribing successful vegetation management treatments in young forest plantations is the absence of vegetation-reduction standards that are quantitatively linked to desired measures of stand performance. This lack of standards generally makes determining the objectives for a particular treatment difficult. Comparing the cost-effectiveness of one treatment with another also becomes difficult.

Response thresholds can be used to evaluate the type and intensity of vegetation treatments that are required to achieve specific management objectives. For example, the rate of herbicide application along the hexazinone gradients produced in Study 2 can be combined with the projected herbaceous leaf-area index to produce a dose-response curve (Fig. 4). This curve can then be used to determine the rates of hexazinone required to achieve the desired thresholds when ponderosa pine is associated with herbaceous vegetation on similar sites. To achieve the maximum-response threshold for pine survival (at a projected herbaceous leaf-area index of 1.5), about 1.0 kg a.i./ha of hexazinone would need to be applied. A forest manager would need to apply hexazinone at rates greater than 1.8 kg a.i./ha to surpass the minimum-response threshold (at a projected herbaceous leaf area index of 0.5) and substantially increase pine stem volume. This type of analytical approach provides a means to evaluate the costs and benefits of various vegetation management options. Integrating competition threshold principles with vegetation treatment effects and costs will be necessary to develop economic threshold concepts for vegetation management (Walstad and Kuch 1987).

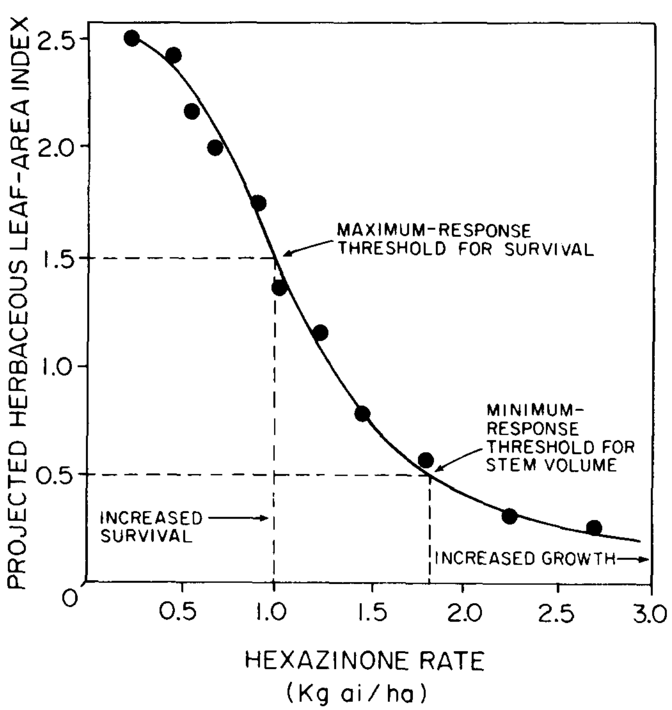

Figure 4. Projected mean herbaceous leaf-area index at the end of one growing season after application of various rates of hexazinone. Each point is the mean of three replications that consisted of nine sample points each. Knowledge of competition thresholds can be used to guide vegetation management prescriptions.

Although the classical definition of an economic threshold indicates a specific weed density at which control measures should be taken, actual calculation of such a threshold is determined from a range of complex factors, uncertainties, and dynamic assumptions (Auld and Tisdell 1986; Cussans et al. 1986; Cousens 1987). Therefore, attempts to calculate precise economic thresholds may be of limited practical value. Further, the definition and utility of various threshold concepts in weed control have been debated (Cussans et al. 1986; Cousens 1987). Cousens (1987) suggests that exactness of definition and application are not essential, and that subjectivity is an acceptable component of weed-control thresholds.

The maximum- and minimum-response thresholds presented in this paper are an extension of the competition threshold concept defined by Cussans et al. (1986) and Cousens (1987). Our subjective selection of the response thresholds for ponderosa pine seedlings is intended, not to provide definitive targets of vegetation abundance for forest management, but to serve as a conceptual guide for evaluating vegetation management strategies and research data. The response-threshold concept suggests that there are levels of vegetation abundance in young forest plantations that need to be

- targeted to achieve specific management objectives, and
- surpassed before appreciable benefits from management inputs can be realized.

Our data indicate that response thresholds will vary depending on the stand parameter of interest. Competition thresholds also are likely to vary from one site to another depending on site quality (Ritchie and Powers 1987), competing species (Larson and Schubert 1969; Elliott and White 1987), seasonal variation (Bridges and Chandler 1987; Bhowmik and Reddy 1988), and the stage of stand development.

Further research on competition thresholds

More research is needed to refine competition threshold concepts in the management of vegetation in young forest plantations. The following points should be considered when forest researchers undertake such studies:

- Controlled experiments should be intentionally created to examine the relation between various levels of associated vegetation and tree performance. Spurious correlations between levels of interspecific competition and tree responses can result when researchers use trees in operational plantations that are "naturally" associated with different levels of interspecific competition (Underwood 1986). Data from experiments designed to compare various kinds of vegetation treatments also may be confounded with site or tree effects associated with the treatments (Ross et al. 1986).

- When controlled experiments are conducted, they should include a full range of competition levels—from no competition to the highest levels of competition encountered in nature. The absence of a full range of competition levels has been a limitation in many plant competition experiments (Firbank and Watkinson 1987). Accurate interpretations of competition in controlled experiments also require an understanding of how plant responses are influenced by the experimental design (Radosevich 1987).

- The shape of the growth curve, and therefore interpretation of interspecific competition thresholds for tree growth, will depend upon the tree-size parameter being examined. For example, it is commonly observed that tree height is less sensitive to levels of competition than stem diameter (Lanner 1985; Zutter et al. 1986; Wagner and Radosevich 1987). Determining size or growth parameters in young trees that are the best indicators of future growth is important to identifying appropriate targets for vegetation management.

- The shape of the growth and survival curves depends on the measure of interspecific competition being used. In most cases, simple measures of density (number of plants per unit area) are inadequate for describing levels of interspecific competition in forest environments. Trees in young plantations are generally surrounded by plants of various species, growth forms, ages, origins, proportions, and spatial arrangements. Research to determine the quantitative measures of vegetation that provide the most accurate estimate of interspecific competitive effects on young trees is needed.

- One of the major limitations to the competition threshold models presented here is their static nature. Static models describe the relation between tree performance and a measure of interspecific competition only after losses in tree growth and survival have occurred. Temporal models that can be used to project future levels of interspecific competition and resulting stand losses will be necessary to appropriately evaluate the cost effectiveness of various vegetation management alternatives.

Conclusions

Ponderosa pine survival and growth decreased in a consistent and systematic manner as levels of interspecific competition increased. Because the effects from neighboring woody and herbaceous vegetation on pines were similar at sites in Oregon and Montana, predictive models, similar to the stand-density models developed for older stands, may be possible for interspecific competition in young plantations. Maximum stem volume of ponderosa pine occurred at substantially lower levels of interspecific competition than maximum survival. Therefore, significant investments in vegetation management beyond those necessary for adequate tree survival may be necessary to obtain significant growth increases.

Threshold concepts that define a level of competing vegetation where maximum tree performance is achieved (maximum-response threshold), and a level of competing vegetation that must be achieved before a substantial response in tree performance can be obtained (minimum-response threshold), provide a means to improve vegetation management in young forest plantations. Better models that predict the effects of various kinds and amounts of interspecific competition on young trees are necessary to refine threshold concepts. Additional controlled experiments are necessary to produce these models.

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